

## Allocation of Resources to Body Components in *Heliocidaris erythrogramma* and *Heliocidaris tuberculata* (Echinodermata: Echinoidea)

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**ABSTRACT**—Adult *Heliocidaris erythrogramma* (*He*) (50 g wet body weight) and *H. tuberculata* (*Ht*) (200 g wet body weight) are compared. The relative sizes of the test and spines are the same for both species, but that of the Aristotle's lantern is 2-fold larger in *He*. The gonad index shows no sexual differences and is similar for both species (*He*: 10, *Ht*: 12). The proximate composition of the gut, Aristotle's lantern, test, and spines of both species are similar. The percent organic material in the ovaries of *He* is greater than in the testes and in the ovaries and testes of *Ht*. Lipid is 50% of the dry weight of the ovaries of *He*, twice that in the ovaries and testes of *Ht*. DNA is 6% of the dry weight of the testes of *He*, half that in the testes of *Ht*. The direct development in *He* and indirect development in *Ht* is correlated with differences in body size and proximate composition of the gonads.

### INTRODUCTION

Grime [11] pointed out the desirability of studying both the established and regenerative phases in the life-history of an organism in considering adaptive strategies, as they may be subject to different forms of natural selection or respond differently to the same selective force. Grime stated these phases are uncoupled, noting the radical differences between larval and adult phases of invertebrates. He suggested a particular regenerative strategy may be modified by two important variables: the strategy adopted during the established phase and the breeding system. A case in point is the genus *Heliocidaris*.

Clark [3] stated the genus *Heliocidaris* A. Agassiz and Desor 1846 contains only two species that differ obviously in general appearance but not in specifics. He separated the species on the basis of number of pore-pairs, a characteristics not expected to cause major functional differences. Among the gross differences is the smaller size of *H. erythrogramma* Valenciennes 1846 (to 86 mm horizontal diameter) compared to *H. tuberculata* Lamarck 1816 (to 106 mm horizontal diameter). The two species differ in habitat. In general, *Heliocidaris erythrogramma* is a rock-burrowing species at low-tide level and *H. tuberculata* is subtidal on the Australian coast and on the reef flat on Lowe Howe Island [3, 4]. The two species probably have different levels of resource availability as well as exposure.

Considerable interest in the two species has resulted from the differences in their development noted by Mortensen [19, 20] and documented by Williams and Anderson [30]. *H. erythrogramma* has direct development in contrast to *H. tuberculata*. Their divergent ontogenies have provided a

model for studying the evolution of development [22]. Studies of the established adult phase have not accompanied these studies.

The ways resources are allocated to structures and functions are important life-history characteristics [2]. Among the most important is the trade-off associated with increased age and size involving a transition to increased allocation to reproduction and decreased allocation to growth. Strathmann & Strathmann [27] noted the association of brooding with small adult-size in marine invertebrates, and pointed out the smaller of co-occurring species are the brooders. None of the hypotheses considered (allometry of egg protection and brood care, longevity with iteroparity, variable recruitment, dispersal) involved the allometry of acquisition and allocation of resources.

Being aware of the difference in size of the established phase of the two species and the trade-off models involving growth and reproduction, we hypothesized allocation of resources to body components in *Heliocidaris erythrogramma* and *H. tuberculata* would differ and that the difference could be correlated with their biology and ecology and with the differences in their regenerative phases. We believe an understanding of the characteristics of the established phase can assist in understanding those of the regenerative phase.

### MATERIALS AND METHODS

*Heliocidaris erythrogramma* were collected at Little Bay on 21 November 1991 and *H. tuberculata* were collected at Shelley Beach, New South Wales, Australia on 7 June and 2 August 1992. These dates are at the maximal gonad indexes of the species' broad reproductive cycles [13]. Individuals were dissected into body compartments that were lyophilized and weighed. The components were homogenized in a Wiley mill for proximate analysis. Ovaries and testes were analyzed separately, but no sexual distinction was made for the somatic compartments as evidence indicates no sexual

differences in echinoids [18]. Lanterns were treated with hydrogen peroxide to obtain the demi-pyramids and rotules by the method of Ebert [5]. Pigmented growth lines in the lantern were counted by the method of Jensen [12] of three specimens of each species. Proximate analysis and calculation of energy equivalents was done by the methods used by Lawrence [14] and Watts and Lawrence [29]. Significant differences were tested by ANOVA except for concentration of DNA, which was compared by Student's *t*-test ( $P < 0.05$ ). Data were transformed as necessary to satisfy conditions of normality and equal variances.

### RESULTS

The sized of the individuals and weights of the body compartments are given in Table 1. Neither *Heliocidaris erythrogramma* or *H. tuberculata* showed sexual dimorphism in size. *Heliocidaris erythrogramma* was smaller than *H. tuberculata*, the difference in weight (4-fold less) being greater than the difference in diameter (1.4-fold less). The weights of the body compartments were correspondingly smaller in *H. erythrogramma* than in *H. tuberculata*. The relative sizes, indexes based on dry weight, did not differ significantly except for the Aristotle's lantern, which was 2-fold greater in *H. erythrogramma* (Table 2). The demi-pyramids of specimens of both species had 4 to 6 pigmented lines, indicating equivalent age and faster growth in *H. tuberculata*.

The proximate composition of the body compartments of the two species (Table 3) are similar except for the gonads.

TABLE 1. *Heliocidaris erythrogramma* and *Heliocidaris tuberculata*: Horizontal diameter (mm); wet body weight and compartment dry weights (g)

	Sex	<i>Heliocidaris erythrogramma</i>	<i>Heliocidaris tuberculata</i>
Horizontal diameter		67 (1) [23]	94 (1) [30]
Wet body weight		53 (2) [23]	201 (6) [30]
Gonads dry weight	M	1.00 (0.32) [9]	6.56 (0.61) [14]
	F	1.22 (0.15) [14]	5.59 (1.76) [9]
Test dry weight		14 (1) [23]	57 (3) [19]
Spines dry weight		16 (1) [23]	63 (3) [20]
Lantern dry weight		1.6 (0.01) [23]	3.2 (0.01) [19]
Rotule dry weight		0.027 (0.001) [19]	0.063 (0.003) [18]
Demi-pyramid dry weight		0.096 (0.004) [19]	0.182 (0.007) [18]

Sexes are combined except for gonads. Means, standard error (in parenthesis), and n (in brackets) are given. All values for the two species are significantly different ( $P < 0.05$ ).

TABLE 2. *Heliocidaris erythrogramma* and *Heliocidaris tuberculata*: Gonad index (% wet body weight); test, spine, and lantern indexes (% dry weight of somatic compartments).

	Sex	<i>Heliocidaris erythrogramma</i>	<i>Heliocidaris tuberculata</i>
Gonad index		9.9 (1.5) [9]	13.3 (0.6) [10]
	F	9.1 (0.7) [14]	11.1 (0.8) [8]
Test index		45 (1) [23]	47 (1) [16]
Spines index		50 (1) [23]	50 (1) [16]
Lantern index		5.3 (0.1) A [23]	2.7 (0.1) B [16]

Sexes are combined except for gonads. Means, standard error (in parenthesis), and n (in brackets) are given. The indexes are not significantly different ( $P > 0.05$ ) except for the lantern index.

TABLE 3. *Heliocidaris erythrogramma* and *Heliocidaris tuberculata*: Proximate composition (% dry weight)

	Sex	<i>Heliocidaris erythrogramma</i>	<i>Heliocidaris tuberculata</i>
Gonads			
% organic material	M	91 (1) [9]	91 (1) [14]
	F	96 (0) [13]	92 (1) [8]
% carbohydrate	M	11 (1) [8]	11 (1) [14]
	F	8 (1) [14]	12 [8]
% lipid	M	26 (2) [9]	22 (1) [13]
	F	50 (2) [14]	27 (1) [9]
% soluble protein	M	37 (3) [9]	42 (2) [13]
	F	29 (2) [14]	45 (3) [9]
% insoluble protein	M	11 [9]	2 [9]
	F	9 [4]	9 [5]
% DNA	M	5.5 (1.9) [4]	14.1 (1.2) B [5]
Test			
% organic material		18 (1) [20]	22 (2) [18]
% carbohydrate		3.21 (0.18) [9]	3.68 (0.35) [9]
% lipid		1.28 (0.04) [12]	1.38 (0.08) [10]
% soluble protein		4.85 (0.28) [12]	4.97 (0.30) [10]
% insoluble protein		9	12

Spines		
% organic material	16 (1) [27]	17 (1) [18]
% carbohydrate	0.36 (0.10) [10]	0.27 (0.02) [10]
% lipid	1.14 (0.10) [12]	0.02 (0.07) [10]
% soluble protein	3.98 (0.30) [12]	2.51 (0.13) [10]
% insoluble protein	11	14
Lantern		
% organic material	20 (1) [20]	24 (2) [19]
% carbohydrate	4.09 (0.32) A	0.78 (0.15) B
% lipid	1.55 (0.10) [12]	1.38 (0.23) [10]
% soluble protein	5.95 (0.68) [12]	1.38 (0.23) [10]
% insoluble protein	9	15

Means, standard error (in parentheses), and n (in brackets) are given. Insoluble protein values were calculated from means. Values with the same letter or no letter are not significantly different.

The ovaries of *H. erythrogramma* had a slight but significantly higher concentration of organic material than those of *H. tuberculata*. This was due to a 2-fold greater concentration of lipid in the ovaries compared to the testes of *H. erythrogramma* and both the ovaries and testes of *H. tuberculata*. The concentrations of the other proximate components in the ovaries of *H. erythrogramma* were correspondingly reduced. The concentration of DNA in the testes of *H. erythrogramma* was one-third that in the testes of *H. tuberculata*.

Most energy in the body compartments was in the form of protein, even in the gonads, except in the ovaries of *Heliocidaris erythrogramma* where most was lipid (Table 4). Most energy in the somatic compartments was in the form of insoluble protein. The ratios of the weights of the wet body and dry somatic components of *Heliocidaris erythrogramma* to *H. tuberculata* were similar, indicating isometry. Likewise the somatic component indexes were similar but the gonad indexes were ca. 2-fold greater in energy units than in gravimetric units for both species.

Five to six growth lines were present on the demipyramids of three specimens of each species.

## DISCUSSION

The established, mature phases of *Heliocidaris erythrogramma* and *H. tuberculata* differ in three major ways: the dimensions and weights of the body and body compartments are smaller in *H. erythrogramma*; the concentration of lipid in the ovaries is greater in *H. erythrogramma* and the concentration of DNA in the testes is less in *H. erythrogramma*; the relative sizes of the body compartments are similar except the Aristotle's lantern index is greater in *H.*

TABLE 4. *Heliocidaris erythrogramma* and *Heliocidaris tuberculata*: Kilojoules in body compartments of females

	<i>Heliocidaris erythrogramma</i>	<i>Heliocidaris tuberculata</i>
Ovaries		
Carbohydrate	1.17	10.63
Soluble protein	8.03	54.56
Insoluble protein	3.54	19.37
Lipid	23.30	54.91
Sum	36.41	139.47
Test		
Carbohydrate	1.37	7.88
Soluble protein	2.83	14.64
Insoluble protein	53.61	266.64
Lipid	1.19	6.72
Sum	59.00	295.88
Spines		
Carbohydrate	0.17	0.51
Soluble protein	2.36	6.38
Insoluble protein	56.92	245.38
Lipid	0.19	<0.01
Sum	60.64	252.27
Lantern		
Carbohydrate	0.17	0.17
Soluble protein	0.47	1.18
Insoluble protein	6.61	16.30
Lipid	<0.01	0.40
Sum	7.25	18.05
Sum all somatic tissues	126.89	566.20
Sum all somatic tissues and ovaries	163.30	705.67
Ovaries/total somatic tissue and ovaries	22	20

*erythrogramma*.

The high concentration of lipid in the ovaries of *Heliocidaris erythrogramma* is at the upper limit reported for the ovaries and eggs of other direct developing echinoderms [8, 15]. Wray & Raff [in 24] reported the eggs of *H. erythrogramma* were ca. 50% lipid by volume. Energy investment per egg would be greater in *H. erythrogramma* than in *H. tuberculata* as a result of the higher concentration of lipid and the larger egg-size.

This is the first report of the concentration of DNA in echinoderm testes. As the sperm-head length of *Heliocidaris erythrogramma* is ca. two-fold greater than that of *H. tuberculata* while the DNA content of the sperm is only ca. 1.3-fold [13, 23], the difference in concentration seems to result from a packing phenomenon. The difference in sperm size affects both energy investment per sperm and sperm number per individual. *Heliocidaris erythrogramma* invests more energy per sperm, and produces fewer sperm per individual as a result of its larger sperm and smaller body size.



Allometry is the general rule with increase in body size [21]. consequently, the isometry of the test, spine, and particularly the gonad indexes of the asymptotic sized of *Heliocidaris erythrogramma* and *H. tuberculata* was not expected. Allometry of the gonads has been reported in several stronglylocentrotid species up to a body size at which isometry occurs [9, 10, 28]. The continued increase in relative gonadal production in *Strongylocentrotus franciscanus* beyond the body size at which it ceases to increase in *S. intermedius* and *S. purpuratus* is correlated with lantern size and allometric coefficient (Lawrence et al., unpub.). Consumption is the largest term in the energy budget and sets the upper limit for all other variables [21]. Assuming the relative size of the lantern is indicative of feeding capacity [5], *H. erythrogramma* should have a greater relative capacity for resource acquisition than *H. tuberculata* at asymptotic body sized. The lantern sizes of similarly-sized (horizontal diameter=60–70 mm) *H. tuberculata* and *H. erythrogramma* are similar (ca. 1.5 g dry weight, Lawrence and Byrne, unpub.).

It seems the conclusion of Strathmann & Strathmann [27] that the species of related co-occurring marine invertebrates that broods has the smaller adults can be extended to species with direct development. This generalization does not address the question of absolute size. *Heliocidaris erythrogramma* is no smaller than the stronglylocentrotid species that have indirect development. If stressful conditions (decreased potential for production) tend to result in the evolution of species that invest more energy per propagule [16, 17], *H. erythrogramma* may have less capacity for production so that it ceases somatic growth at a smaller size, and makes up for decreased fecundity by direct development. These considerations fit Ebert's [6] conclusion that *H. erythrogramma* is a very long-lived species. The longevity of *H. tuberculata* is not known. The similar number of growth lines but different body sizes indicates *H. tuberculata* grows more rapidly than *H. erythrogramma*. Overall, the differences in asymptotic body size, growth rates, and fecundity between the two species seem related to their potential for production.

Growth has both genetic and environmental controls [25]. Although echinoids fit the indeterminate growth pattern (plastic asymptotic, growth), in which the growth trajectory and adult size are determined by energy intake and costs, a genetic component exists as seen here with the two species of *Heliocidaris*. We assume the difference in growth rates and asymptotic sizes of *Heliocidaris erythrogramma* and *H. tuberculata* involved the evolution of genetic control of growth patterns. The difference in developmental pattern in *H. erythrogramma* involved the evolution of genetic control of developmental processes [22]. Did the evolution of both the regenerative and established phase occur simultaneously or sequentially? If indirect development is lost more frequently than gained evolutionarily [7, 8, 26], the direction of evolution was from *H. tuberculata* to *H. erythrogramma*.

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## REFERENCES

- 1 Brody S (1945) Bioenergetics and Growth. Hafner Publishing Company, New York, pp 1023
- 2 Calow P (1984) Economics of ontogeny—adaptational aspects. In "Evolutionary Ecology" Ed by B Shorrocks, Blackwell Scientific Publications, Oxford, pp 81–104
- 3 Clark HL (1946) The echinoderm fauna of Australia: its composition and origin. Carnegie Inst Wash Pub 566, pp 567
- 4 Dakin WJ (1952) Australian Seashores. Angus and Robertson, Sydney, p 372
- 5 Ebert TA (1980) Relative growth of sea urchin jaws: an example of plastic resource allocation. Bull Mar Sci 30: 467–474
- 6 Ebert TA (1982) Longevity, life history, and relative body wall size in sea urchins. Ecol Monogr 52: 353–394
- 7 Emlet RB (1990) World patterns of developmental mode in echinoid echinoderms. Adv Invert Reprod 5: 329–335
- 8 Emlet RB, McEdward LR, Strathmann RR (1987) Echinoderm larval ecology viewed from the egg. Echinoderm Studies 2: 55–136
- 9 Fuji A (1967) Ecological studies on the growth and food consumption of Japanese common littoral sea urchin, (*Strongylocentrotus intermedius*) (A. Agassiz). Mem Fac Fish Hokkaido Univ 15: 83–160
- 10 Gonor JJ (1972) Gonad growth in the sea urchin (*Strongylocentrotus purpuratus*) (Stimpson) (Echinodermata: Echinoidea) and the assumptions of the gonad index methods. J Exp Mar Biol Ecol 10: 89–103
- 11 Grime JP (1979) Plant strategies and vegetation. John Wiley & Sons, Chichester
- 12 Jensen M (1969) Age determination of echinoids. Sarsia 37: 41–44
- 13 Laegdsgaard P, Byrne M, Anderson DT (1991) Reproduction of sympatric populations of *Heliocidaris erythrogramma* and *H. tuberculata* (Echinoidea) in New South Wales. Mar Biol 110: 359–374
- 14 Lawrence JM (1973) Level, content, and caloric equivalents of the lipid, carbohydrate, and protein in the body components of *Luidia clathrata* (Echinodermata: Asteroidea: Platyasterida) in Tampa Bay. J Exp Mar Biol Ecol 11: 263–274
- 15 Lawrence JM (1987) A Functional Biology of Echinoderms. Crooms-Helm, London, p 340
- 16 Lawrence JM (1990) The effect of stress and disturbance on echinoderms. Zool Sci 7: 17–28
- 17 Lawrence JM (1991) Analysis of characteristics of echinoderms associated with stress. In "Biology of Echinodermata" Ed by T Yanagisawa, I Yasumasu, C Oguro, N Suzuki, T Motokawa, Balkema, Rotterdam, pp 11–26
- 18 Lawrence JM, Lane JM (1982) The utilization of nutrients by postmetamorphic echinoderms. In "Echinoderm Nutrition" Ed by M Jangoux, JM Lawrence, Balkema, Rotterdam, pp 331–371
- 19 Mortensen TH (1915) Preliminary note on the remarkable, shortened development of an Australian sea-urchin, *Toxocidaris erythrogramma*. Proc Linn Soc N S Wales 40: 203–206
- 20 Mortensen TH (1921) Studies of the development and larval

- forms of echinoderms. IV. K Danske Vidensk Selsk (Naturvid Math Afd Ser 9) 7(3): 1-59
- 21 Peters RH (1983) The Ecological Implications of Body Size. Cambridge Univ. Press, Cambridge
- 22 Raff RA (1992) Direct-developing sea urchins and the evolutionary reorganization of early development. *Bio Essays* 14: 211-218
- 23 Raff RA, Herlands L, Morris VB, Healy J (1990) Evolutionary modification of echinoid sperm correlates with developmental mode. *Dev Growth Diff* 32: 283-291
- 24 Scott LB, Lennarz WJ, Raff RA, Wray GA (1990) The "lecithotrophic" sea urchin *Heliocidaris erythrogramma* lacks typical yolk platelets and yolk glycoproteins. *Develop Biol* 138, 188-193
- 25 Sebens KP (1987) The ecology of indeterminate growth in animals. *Ann Rev Ecol Syst* 18: 371-407
- 26 Strathmann RR (1987) The evolution and loss of larval feeding stages of marine invertebrates. *Evolution* 32: 894-906
- 27 Strathmann RR, Strathmann MF (1982) The relationship between adult size and brooding in marine invertebrates. *Am Nat* 119: 91-101
- 28 Tegner MJ, Levin LA (1983) Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *J Exp Mar Biol Ecol* 73: 125-150
- 29 Watts SA, Lawrence JM (1985) The effect of feeding and starvation on the level and content of nucleic acids in the pyloric caeca of *Luidia clathrata* (Say). In "Echinodermata" Ed by BF Keegan & BDS O'Connor, Balkema, Rotterdam, pp 571-576
- 30 Williams DHC, Anderson DT (1975) The reproductive system, embryonic development, larval development and metamorphosis of the sea urchin *Heliocidaris erythrogramma*. *Aust J Zool* 23: 371-403